CHAPTER 14

Nutritional Value of Potatoes: Vitamin, Phytonutrient, and Mineral Content

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14.1 Introduction

Potatoes were domesticated between 7000–10 000 years ago, likely around Lake Titicaca, an alpine lake at 12 500 feet in the Andes between Peru and Bolivia (Spooner et al., 2005). Potatoes may contain more genetic diversity than any other crop and this may reflect the ability of potatoes to grow in remarkably divergent environments, from arid alpine highlands to tropical rainforests to permafrost soils just below the Arctic Circle and even on tree branches (Hawkes, 1990). This genetic diversity is a valuable resource towards further improving tuber nutritional content, especially when taking into account that modern cultivars are estimated to contain less than 1% of the available genetic diversity of wild species. About 200 wild potato species exist, in addition to thousands of primitive varieties. Potatoes are the fourth most grown crop in the world, after the cereals rice, wheat, and maize and are the only major food crop that is a tuber.

Potato tubers are highly specialized organs evolved to improve a plant's chances of survival and to allow vegetative reproduction. Tubers are not derived from roots, but are modified stems, originating on stolons from axillary buds on the underground part of the stem (Ewing and Struik, 1992; Fernie and Willmitzer, 2001; Jackson, 1999). The fact that tubers are modified stems influences tuber characteristics and chemical composition. For example, the greening of tubers that occurs on exposure to light in which amyloplasts in the tuber parenchyma redifferentiate into chloroplasts (Deng and Gruissem, 1988), reflects the stem origin of the tuber. Tubers are metabolically active, contain an abundant amount of plastids and synthesize numerous compounds derived from plastidic biosynthetic pathways. Indeed, the complex metabolite composition of tubers belies their misperception as simple organs containing starch and not much else.

In fact, tubers contain plentiful amounts of small molecules and secondary metabolites, which have roles in an array of key tuber processes from regulating tuber organogenesis to mediating responses to the environment. Moreover, many of these compounds have positive effects on human health and are highly desirable in the diet (Flamini, 2003; Katan and De Roos, 2004).

14.2 The Dietary Importance of Potatoes

Potatoes are uniquely positioned to be a valuable source of dietary vitamins, minerals, and phytonutrients because of their per capita consumption. In most of the developed world, potatoes are by far the most eaten vegetable (Figure 14.1). Because of this high consumption the vitamin and phytonutrient content of potato will have much more dietary relevance and impact than foods eaten in sparse quantities. Moreover, in the developing world, potato consumption is increasing at about 5% a year and in 2005 the developing world for the first time produced more potatoes than the developed world. China and India produce about one third of the world's potatoes.

Potatoes yield more calories per acre than any other major crop, a criterion that becomes even more important in light of the planet's ever-increasing population, food shortages, price spikes, and the recent competition for farmland by biofuel crops. Collectively, these facts emphasize the impact potatoes can have on global nutrition.

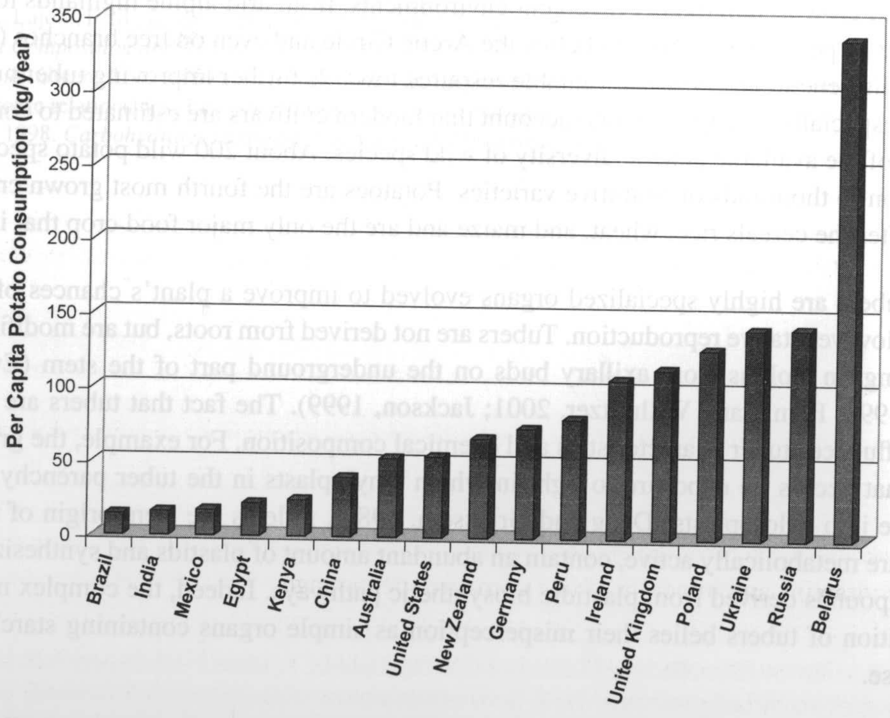


Figure 14.1: Per capita consumption of potatoes in 17 countries in 2005. Based on numbers reported by the Food and Agricultural Organization of the United Nations.

14.3 Popular Diets and Potato Consumption

Unlike during most of its long gastronomic history, the nutritional qualities of potatoes are perhaps currently under-appreciated due to negative publicity from various sources, such as low-carbohydrate diet advocates. The recent popularity of low-carbohydrate diets has impacted consumption of traditional staples such as potatoes, rice, bread, and pasta. Million dollar marketing campaigns have been launched in recent years to promote the nutritional advantages of potato, including the British Potato Council's 'Fab not Fad' marketing campaign that aggressively criticized 'fad diets.'

Recent years have shown that consumer perception about the nutritional value of potatoes impacts sales and strongly suggests that perceived nutritional value is a very important trait for any vegetable, especially potatoes given the recent negative publicity. A growing number of consumers appear increasingly interested in the medicinal benefits of foods and the relationship between diet and health. It has been estimated that one third of Americans take a daily vitamin or dietary supplement and annual supplement sales in the US top 18 billion dollars. Furthermore, in the years ahead, medical research will discover much more about which plant nutrients have positive effects on health, drawing more attention to the diet–health link.

Generally, crops have been bred and selected primarily for traits such as yield, disease resistance, and appearance. Historically, little effort has been directed towards increasing the nutritive value of any crop for reasons including that there were more pressing issues, plus the daunting technical difficulty of such an undertaking. With most crops, including potatoes, nutrient profiles are available only for a few varieties. Thus, surprisingly little is known about just what vitamins and nutrients are in potatoes. Which varieties have the most? Can new varieties be developed that have even more? Answering these types of questions has been made easier due to recent technological advances, like high-throughput assays, affordable and powerful mass spectrometers, and myriad molecular biological tools.

14.4 Tuber Composition

Potatoes are approximately 80% water and 20% solids, although this can vary by several percentage points depending on the cultivar. Of the 20 grams of solids in a 100 gram tuber, about 18 grams are carbohydrate and 2 grams protein. The primary storage proteins in tubers are patatins, which account for 40% of the soluble protein content (Prat, 1990). Potatoes are a good source of many vitamins and minerals; if one compares percentage of recommended daily allowance (RDA) of calories in a given portion size versus the percentage of the RDA of vitamins and minerals in that same portion, many vitamins and minerals exceed the percentage of calories. For example, according to the USDA nutrient database, 100 grams (3.5 ounces) of potatoes contains 4% of the RDA calorie intake, 33% of the RDA of vitamin C, the most abundant vitamin in potatoes and 12% of the RDA for potassium.

In addition to vitamins and minerals, tubers contain a complex assortment of other small molecules, many of which are phytonutrients. These include polyphenols, flavonols, anthocyanins, phenolic acids, carotenoids, polyamines, glycoalkaloids, tocopherols, calystegines, and sesquiterpenes.

14.5 Vitamin C

Potatoes are a well-known source of vitamin C, with a medium red-skinned potato (173 grams) providing about 36% of the RDA according to the USDA databases. Vitamin C has a major role in detoxifying reactive oxygen species in plants, which are the primary source of vitamin C in the human diet. Leafs and chloroplasts can contain 5 to 25 mM L-ascorbate, respectively (Wheeler et al., 1998). Plants may have multiple vitamin C biosynthetic pathways, with all of the enzymes of the L-galactose pathway recently characterized (Laing et al., 2007; Wolucka and Montagu, 2007). Vitamin C is a cofactor for numerous enzymes, functioning as an electron donor. The best known symptom of vitamin C deficiency is scurvy, which in severe cases is typified by loss of teeth, liver spots, and bleeding.

One study examined tuber vitamin C content in 75 genotypes and found concentrations ranging from 11.5 to 29.8 mg/100 g FW (Love et al., 2004). This study also reported that some genotypes had more consistent concentrations of vitamin C than others across multiple years or when grown in different locations and suggests that the year may have a bigger effect than location. A British study measured vitamin C in 33 cultivars grown in three locations around Europe (Dale et al., 2003). If these author's results in dry weight are converted to fresh weight assuming potatoes are 80% water, a range of 13–30.8 mg vitamin C per 100 grams FW is obtained, which is consistent with the Love et al. report.

Numerous studies have shown that vitamin C levels decrease rapidly during cold storage of potatoes and losses can approach a 60% decrease (Keijbets and Ebbenhorst-Seller, 1990). After placing 33 genotypes in cold storage for 15–17 weeks, Dale et al. found substantial decreases in vitamin C compared to pre-storage (Dale et al., 2003). Vitamin C decreases ranged from 20–60% depending on the genotype. The authors make the important point that breeding efforts to increase vitamin C should focus on post-storage content and that in most cases this is more relevant than fresh-harvest concentrations. This will be truer for countries that place a majority of the potato harvest in cold storage than for developing countries that make limited use of cold storage and for which post-harvest loses consequently should be less.

A Turkish study examined the effect of freeze-storing peeled, blanched then fried potatoes and found a 10% loss of vitamin C after 6 months of storage at −18°C (Tosun and Yücecan, 2008). However, a 51% loss was caused by the pre-freezing operations, which sounds a cautionary note about the importance of how potatoes are handled during processing. Some of our own cooking studies with skin-on potatoes using microwaving, steaming, baking, and boiling have shown a negligible loss of vitamin C. Thus, in the absence of cultivars with stable vitamin C levels during cold storage, one solution that may help to minimize post-harvest loss of vitamin C for some commercial products would be minimally destructive cooking of tubers shortly after harvest, followed by flash-freezing of the product.

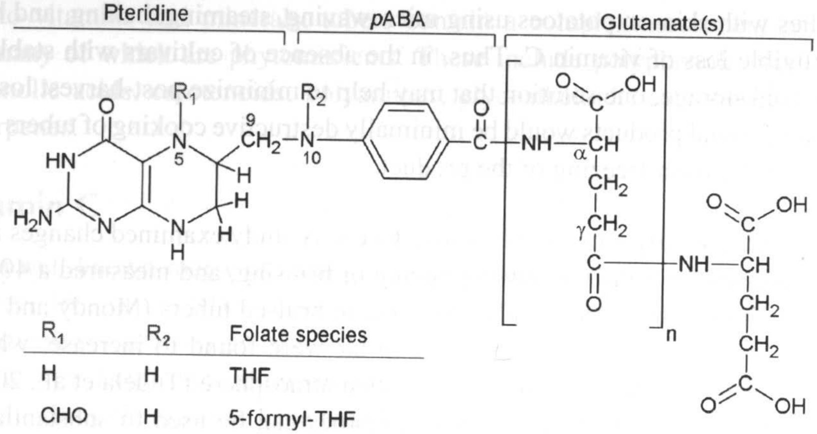
Wounding can substantially increase vitamin C levels. A study examined changes in vitamin C after storing potatoes for 2 days following slicing or bruising, and measured a 400% increase in vitamin C in sliced tubers, but a 347% decrease in bruised tubers (Mondy and Leja, 1986). Vitamin C levels in fresh-cut potatoes stored in air were found to increase, whereas levels decreased in those stored frozen or under a modified atmosphere (Tudela et al., 2002b). These and similar results suggest that wounding of potatoes can be used to substantially increase vitamin C in commercial products. However before this is likely to be widely adopted as a strategy to increase vitamin C, a method must be found to decrease the browning that can occur in cut tissue and which consumers find undesirable.

14.6 Folate

Folates (vitamin B9) is a generic name commonly used to design tetrahydrofolate (THF) and its one-carbon (C1) unit derivatives (Figure 14.2). Folates are important cofactors involved in C1 unit transfer reactions. Two crucial pathways occurring in mammalian and plant cells that involve C1 unit transfer reactions are DNA biosynthesis and the 'methylation cycle' (Scott, 1999). Folates are essential micronutrients in the human diet. Indeed, while plants and microorganisms can synthesize folates, humans lack this ability and require a dietary supply. Plants represent the major source of folate in the diet.

14.6.1 Importance of potato folate in the diet

Potato is a well-known significant source of folates in the diet due to its high level of consumption more so than for its endogenous content. In the Netherlands, Brussaard et al. (1997) reported that potatoes, among vegetables, were the most important source of folate in the diet, supplying 10% of the total folate intake. Potatoes were the third most important overall source of folate in the Dutch diet, providing 7% of the total folate intake (Konings et al., 2001). Potatoes provided 9–12% of the total folate intake in a Norwegian study (Brevik et al., 2005). In Finland, potatoes were among the best source of folate in the diet (Vahteristo et al., 1997) providing ~10% of the total folate intake (Alfthan et al., 2003). In a Spanish subpopulation, potatoes provided 3.6% of the total folate intake (Plannels et al., 2003). Hatzis et al. (2006) examined the association between serum folate status and food consumption in a Greek population and showed that increased consumption of potatoes was associated with decreased risk for low serum folate.



R_1	R_2	Folate species
H	H	THF
CHO	H	5-formyl-THF
H	CHO	10-formyl-THF
CH_3	H	5-methyl-THF
=CH-		5,10-methenyl-THF
$-CH_2-$		5,10-methylene-THF

Figure 14.2: Chemical structure of folates. Folate molecules consist of pteridine, para-aminobenzoate (pABA), and glutamate moieties. Plants usually contain polyglutamylated forms of folates that are made by the addition of up to about six glutamate residues (which form the γ-glutamate tail) attached to the first glutamate, each linked by amide bonds to the preceding molecule of glutamate through the γ-carboxyl of the latter. C1 units at various levels of oxidation can be attached to N5 and/or N10, as indicated by R_1 and R_2.

14.6.2 Folate concentrations in potato and other crops

Several studies reported folate concentrations in potatoes of usually unspecified genotypes and the reported values can vary substantially depending on the analytical method used (Konings et al., 2001). Values for folate concentrations in mature raw potato vary between 12 and 37 μg/100 g FW (Holland et al., 1996; Konings et al., 2001; Vahteristo et al., 1997) except in a study by McKillop et al. (2002) who reported an exceptionally high folate concentration (125 μg/100 g FW). The USDA National Nutrient Database for Standard Reference (SR20) gives values of 14 and 18 μg/100 g FW for raw potatoes. Recently, we determined total folate concentrations of potato tubers from >70 cultivars, advanced breeding lines, and wild species and found values ranging from 0.46 to 1.37 μg/g DW or 11 to 35 μg/100 g FW (Goyer and Navarre, 2007 and unpublished). Seven of the top ten varieties were yellow-fleshed, two were red-fleshed and one was white-fleshed. Yellow color was not always associated with high folate content since yellow-fleshed cultivars covered the whole range of folate concentrations. Cultivars Winema and Ranger Russet had the highest amounts of folate among white-fleshed cultivars (0.95 and 1.04 μg/g DW, respectively). Among the top yellow cultivars were Golden

Sunburst, Satina, and Carola (1.19, 1.25, and 1.37 μg/g DW, respectively). Colorado Rose was the top red-fleshed cultivar (1.03 μg/g DW). Also in the top 10 were breeding lines from Washington, Oregon, and Colorado. Genotypes *Solanum pinnatisectum* and Gayna had the highest folate concentrations among wild species and primitive germplasm (0.99 and 1.05 μg/g DW) and *S. pinnatisectum* also had the highest folate content of all genotypes analyzed on a fresh weight basis (0.35 μg/g FW). Despites the small number of wild species analyzed (12), an approximately two-fold difference between the lowest and the highest genotypes was found, suggesting that among the large number of existing indigenous potato species there might be some with even higher folate concentrations.

Potato is in the lower range of folate contents among plant foods (Table 14.1) as are other underground organs, ranking ahead of polished rice but behind green leafy vegetables and pulses. A number of factors may affect the bioavailability of folates from plant foods. These

Table 14.1: Folate content in various plant foods. All values are given for raw food. References for the lowest and the highest folate content values are indicated

Crop	Folate content (μg 100/g FW)	References
Rice (white unenriched)	6-9	1
Sweet potato	11	1
Onions	10–19	2, 1
Tomato	8–30	2, 1
Potato	11–37 (125? Ref. 5)	3, 4, 5
Banana	13–20	6, 1
Carrot	16–19	6, 1
Corn (yellow)	19	1
Orange (peeled)	18–30	2, 1
Cassava	27	1
Peas (green)	25–65	7, 1
Strawberry	13–96	8
Snap beans	37	1
Wheat (hard, white)	38	1
Lettuce (fresh)	38–43	1, 2
Corn (sweet, white or yellow)	46	1
Rye (grain)	60–78	1, 9
Wild rice	95	1
Broccoli	63–114	1, 6
Spinach	100–194	2, 1
Peanut	110–240	4, 1
Lentils	151–479	7, 1
Beans (navy, pinto, Great Northern)	143–525	7, 1

References: 1, The USDA National Nutrient Database for Standard Reference (SR20) http://www.ars.usda.gov/main/site_main.htm?modecode=12354500; 2, Konings et al., 2001; 3, Goyer and Navarre, 2007; 4, Holland et al., 1996; 5, McKillop et al., 2002; 6, Vahteristo et al., 1997; 7, Han and Tyler, 2003; 8, Tulipani et al., 2008; 9, Kariluoto et al., 2001.

include the instability of certain labile folate derivatives during digestion, the food matrix, the presence of food constituents that may enhance folate stability during digestion, and the efficiency of intestinal deconjugation of polyglutamylated folates to monoglutamates for normal absorption in the proximal small intestine.

14.6.3 Folate derivatives composition and glutamylation levels in potato tubers

All native reduced folate derivatives are very sensitive to oxidative cleavage at the C9 and N10 bond (Figure 14.2), however there are marked differences in stability of those species, 5-formyl-THF being the most stable natural folate, THF the least, and 5-methyl-THF intermediate (Forssén et al., 2000). Polyglutamates must be hydrolyzed to the respective monoglutamylated forms by folate deconjugase before absorption by the intestine, but it remains controversial whether polyglutamates are less bioavailable than monoglutamates (McNulty and Pentieva, 2004). Vahteristo et al. (1997) determined that raw potatoes contained 21 μg/100 g FW of 5-methyl-THF, 3 μg/100 g FW of THF, and traces of 10-formyl-folic acid, an oxidation product of 10-formyl-THF. Konings et al. (2001) showed that >95% of folates were present as a 5-methyl-THF derivative in potato tubers, the rest comprising 10-formyl-folic acid and folic acid, and that total folate derivatives were >90% polyglutamylated. Therefore, polyglutamylated forms of 5-methyl-THF seem to constitute most of the folate pool in potato tuber as is the case in most fruits and vegetables (de la Garza et al., 2004; Freisleben et al., 2003; Konings et al., 2001; Orsomando et al., 2005; Storozhenko et al., 2007; Vahteristo et al., 1997).

14.6.4 Food matrix

Folates can be covalently bound to macromolecules of the food matrix and entrapped folates must be released from plant cellular structure before absorption by the intestine. There is little information on how much matrix-bound folates are in potato. While Konings et al. (2001) reported that the addition of protease and amylase did not significantly increase folate content values in potato, we found that protease treatment followed by amylase and conjugase gave folate values ~20% higher than when protease treatment was performed last, indicating that a significant amount of protein-bound folates became accessible to conjugase after protease treatment (Goyer and Navarre, unpublished).

14.6.5 Stabilizers

Some dietary constituents may protect folate against degradation during digestion (as well as during processing and cooking). Binding of folates to folate-dependent proteins (e.g. T-protein of glycine decarboxylase) greatly improves their stability (Rébeillé et al., 1994). Antioxidants such as ascorbic acid or thiol compounds also protect folates against oxidative degradation (McNulty and Pentieva, 2004). It is noteworthy that potato is a good source of vitamin C.

14.6.6 Effect of storage, processing, and cooking on folates

A significant amount of literature exists regarding the effects of storage, processing, and cooking on folate retention in some vegetables, legumes, and cereals (Kariluoto et al., 2006; Melse-Boonstra et al., 2002; Scott et al., 2000; Strålsjö et al., 2003). In contrast, there is little information on the effects of storage and processing on folate contents in potato and most of the available information concerns the effect of cooking. McKillop et al. (2002) showed that boiling of whole potatoes for 60 minutes resulted in a less than 20% decrease in folate content whether or not skin was retained during boiling. Konings et al. (2001) reported folate concentrations for cooked French fries, boiled potatoes and fried potatoes that were similar to those in raw potatoes (16% increase, and 25 and 8% decreases, respectively).

Earlier reports by Vahteristo et al. (1997) showed 35 and 52% decrease in French fries and boiled potato compared to raw potatoes. Augustin et al. (1978a) examined the effect of four cooking methods on folate concentrations in four different potato cultivars and showed that overall retention of folate was >70%. However, retention was cultivar-dependent, Norchip and Pontiac having the lowest retention values (e.g. 46% for boiled, peeled, Pontiac samples) and Russet Burbank and Katahdin the highest. Boiled, peeled samples had consistently lower folate concentrations than boiled unpeeled samples. In addition to its positive effect on folate retention, skin has higher folate concentrations than flesh (Augustin et al., 1979; Goyer and Navarre, 2007). The highest retention values were always obtained from unpeeled boiled or microwaved samples, with a few cases where boiling or microwaving led to an increase in folate concentrations compared to raw tubers (maximum 111% increase). Oven-baked potatoes had the lowest overall retention values.

14.6.7 Strategies towards improving folate content and bioavailability in plant foods

Folate deficiency is associated with the increased risk of neural tube defects (spina bifida, anencephaly), cardiovascular diseases, megaloblastic anemia, and some cancers (Bailey et al., 2003; Finglas et al., 2006; Scott et al., 1999). Unfortunately, folate intake is suboptimal in most of the world's populations, even in developed countries (Scott et al., 2000). Therefore there is an urgent need to increase folate content and bioavailability in staple foods. Because of its large consumption worldwide, potato is an appealing target for enrichment.

Folate biosynthesis has been well delineated in recent years, enabling metabolic engineering of the pathway. Successes in enhancing folate production in tomato fruit and rice grain by over-expressing the first enzyme of both the para-aminobenzoic acid and the pteridine branches of the folate pathway were recently reported (Díaz de la Garza et al., 2007; Storozhenko et al., 2007), and the strategy is well in place to be implemented in other crops such as potato tubers which contain all the genes necessary for folate biosynthesis. Other possible strategies for metabolic engineering were described in detail in recent reviews (Basset et al., 2005;

Bekaert et al., 2007; Rébeillé et al., 2006) and include increasing the proportion of 5-formyl-THF, the most stable natural folate, sequestering folates into vacuoles, increasing folate salvage capacity or over-expressing folate-binding protein of plant (yet to be identified) or mammalian (Jones and Nixon, 2002) origin in plant cells.

Natural variation of folate concentration among germplasm within a species has been reported for a number of crops and could be exploited in breeding programs to increase folate concentrations in crops. We showed an approximately three-fold difference in folate values amongst >70 potato genotypes (Goyer and Navarre, 2007). An ~7.5-fold difference in folate values was reported amongst nine strawberry genotypes (Tulipani et al., 2008). Smaller variations were reported for pulses and rye (Han and Tyler, 2003; Kariluoto et al., 2001) but only very few genotypes were analyzed in each case.

Household strategies to improve the bioavailability of folates from foods have been suggested especially for developing countries where folic acid supplementation and food fortification remain far from accessible (Gibson et al., 2006). Thermal processing generally increases the digestibility of proteins and carbohydrates and therefore the release of folates from the food matrix. Combining ingestion of certain foods in the diet, for instance foods rich in antioxidants, may also improve the stability of folates. Various potato germplasm has markedly different antioxidant properties (Brown et al., 2005; Dale et al., 2003) and consumption of high antioxidant genotypes, independently of their endogenous folate contents, may provide larger amounts of bioavailable folates than those with lower antioxidants contents.

14.7 Vitamin B6

Like folate and vitamin C, vitamin B6 (pyroxidine) is water soluble and like folate has several vitamers. Vitamin B6 may be involved in more bodily functions than any other nutrient (Tambasco-Studart et al., 2005), is a cofactor for many enzymes, especially those involved in protein metabolism, and is also a cofactor for folate metabolism. Vitamin B6 has anticancer activity (Theodoratou et al., 2008), is a strong antioxidant (Denslow et al., 2005), is involved in hemoglobin biosynthesis, lipid and glucose metabolism and immune and nervous system function. Possible consequences of deficiency include anemia, impaired immune function, depression, confusion, and dermatitis (Spinneker et al., 2007). Vitamin B6 deficiency is generally not a problem in the developed world, but there could be as yet poorly defined consequences of suboptimal intake particularly for the elderly.

Potatoes are an important source of dietary vitamin B6 (Kant and Block, 1990) with a medium baked potato (173 grams) providing about 26% of the RDA (USDA National Nutrient Database SR20). Very little research has been conducted on this vitamin in potato, thus little is known about how much its concentrations vary among genotypes; ranges of 0.26–0.82 mg/200 g FW have been reported (Rogan et al., 2000). One study found that its concentration increased during storage (Augustin et al., 1978) and that losses were less than 10% during cooking (Augustin et al., 1980).

Recently much has been learned about vitamin B6 synthesis in plants including identification of the key genes *PDX1* and *PDX2* (Tambasco-Studart et al., 2005). Such information should enable new approaches to further enhance vitamin B6 concentrations in potatoes.

14.8 Glycoalkaloids

Potentially toxic compounds called glycoalkaloids (GAs) are found in many members of the Solanaceae, including potatoes, eggplants, and tomatoes. GAs are secondary metabolites and their role in plants is to contribute to pest and pathogen resistance. From a dietary standpoint, GAs are regarded as anti-nutritive compounds capable of causing vomiting and other ill effects if ingested in high enough amounts (Hopkins, 1995; McMillan and Thompson, 1979). Another undesirable trait is that GAs can contribute a bitter taste at higher concentrations (Sinden et al., 1976). Newly developed potato varieties in the United States must contain less than 20 mg/100 gram fresh weight (FW) of total GAs (Wilson, 1959) but the guidelines established in other countries vary. However, as discussed below, the assumption that GAs are categorically undesirable in the diet is complicated by recent studies that show some GAs have health-promoting effects. Thus a more nuanced approached to tuber GA content may be in order.

14.8.1 Glycoalkaloid biosynthesis

Potato GAs are steroidal alkaloids comprised of a heterocyclic nitrogen, and a C27 steroid conjugated to a sugar moiety, most commonly a tri- or tetrasaccharide. The GA biosynthetic pathway is not fully delineated, even for solanine and chaconine, the major potato GAs. GAs are derived from the mevalonate pathway via cholesterol (Heftmann, 1983; Johnson et al., 1963), occur throughout the tuber, but are primarily synthesized in the phelloderm (Krits et al., 2007). The nitrogen is suggested to be derived from arginine (Kaneko et al., 1976). GAs are found in much higher concentrations in leaves, sprouts, and fruit than in tubers. GA concentrations approaching 18 grams/kg FW have been reported in sprouts (Valkonen et al., 1996).

Much remains to be elucidated about the genes and enzymology involved in conversion of cholesterol into the various GAs. Various glycosylation steps and several glycosyltransferases have been characterized or cloned (McCue et al., 2007; Moehs et al., 1997; Stapleton et al., 1991; Zimowski, 1991). Identification of these GA biosynthetic genes has enabled transgenic approaches to decrease potato GA content. Potatoes overexpressing a soybean sterol methyltransferase exhibited decreased amounts of GAs (Arnqvist et al., 2003), while antisense expression of several potato steroidal glycosyltransferases reduced GA levels (McCue et al., 2005, 2007).

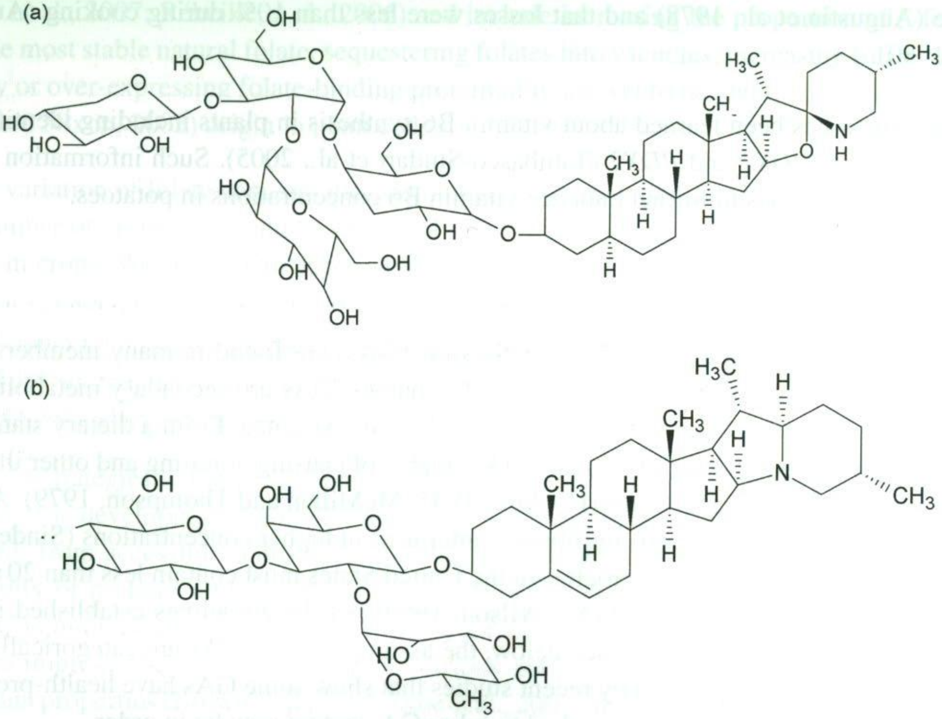


Figure 14.3: Potato glycoalkaloids. (a) is tomatine, a spirosolane and (b) solanine, a solanidane.

14.8.2 Types of potato GAs

Potato GAs usually belong to one of two structural types, either solanidanes or spirosolanes (Figure 14.3). Solanine and chaconine, both solanidanes, often comprise upwards of 90% of the total GA complement of domesticated potatoes, with chaconine often more abundant than solanine (Griffiths et al., 1997; Sotelo and Serrano, 2000).

Many in the potato industry may be familiar only with solanine and chaconine, but estimates have been made that the potato family, including wild species, may contain about 90 GAs (Friedman and McDonald, 1997). In the course of LCMS characterization of small molecule diversity in tubers from diverse potato germplasm, we observed that GAs constituted a major source of diversity.

Mass spectrometry is well suited to GA analysis and is much more selective and sensitive than many methods used to analyze GAs. In our study of tubers from four wild potato species and three cultivars, about 100 GAs were tentatively identified (Shakya and Navarre, unpublished results). This number of GAs was unexpected, especially when considering only seven genotypes were analyzed and that only tubers were used, which have much lower GA concentrations than leaves, sprouts, flowers, or leaves. Consequently, potatoes may have a much greater diversity of GAs than previously realized. This GA diversity may offer opportunities for the production of future varieties with a more optimal GA compliment. The predominance of solanine and chaconine in modern Western cultivars may be due to the fact that only a tiny percentage of available potato germplasm was used in the breeding of these cultivars and reflects something of a bottleneck in the genetic diversity of commercial cultivars.

14.8.3 Toxic effects of GAs

The effects on humans of eating potatoes with high GA concentrations have been well documented (Friedman, 2006). Symptoms can include cramping, diarrhea, vomiting, sweating, rapid pulse, and coma. The physiological effects of GAs are mainly a consequence of their disruption of cell membranes and inhibition of cholinesterase activity. Estimates have varied about the amount of GAs needed to be ingested to have toxic effects, with 1–5 mg/kg of body weight one suggested range, which is roughly equivalent to that of strychnine (Mensinga et al., 2005; Morris and Lee, 1984). Doses as low as 5–6 mg/kg body weight may be lethal (Morris and Lee, 1984).

Chaconine is more toxic than solanine and these two GAs become less toxic with progressive loss of sugars, with the aglycone being the least toxic (Friedman and McDonald, 1997). An important determinant of GA cholinesterase inhibitory activity seems to be the E and F rings of the aglycone (Roddick et al., 2001). In general solanidanes seem to be more toxic than spirosolanes. Friedman has suggested replacing solanidine and chaconine in potatoes with the less toxic tomatine (Friedman, 2002), which also has health-promoting properties. Such a goal could perhaps be accomplished by transgenic approaches or by identifying potato genotypes with low solanidine/chaconine and high tomatine.

14.8.4 Health-promoting effects of GAs

Health-promoting effects of GAs have been reported for several decades, such as inhibition of mice sarcoma tumors by a solamarine (Kupchan et al., 1965). The spirosolane, solasodine, may protect against skin cancer (Cham, 1994). Recent studies have convincingly shown that some GAs have anticancer properties. GAs including tomatine, solanine, and chaconine were shown to inhibit growth of human colon and liver cancer cells in cell culture assays (Friedman et al., 2005; Lee et al., 2004) with a potency similar to the anticancer drug adriamycin. Anticancer effects were also seen in assays using cervical, lymphoma, and stomach cancer cells and treatments using two or more GAs suggested both synergistic and additive effects (Friedman et al., 2005).

A key question that cannot be answered using cell culture assays is whether dietary GAs can have similar effects. Importantly, evidence that dietary tomatine is effective against cancer was shown in a feeding study using rainbow trout, in which reduced tumor incidence was found in tomatine-fed trout (Friedman et al., 2007). Tomatidine has potential as a chemosensitizing agent, increasing the effectiveness of cancer chemotherapy by inhibiting multidrug resistance in human cancer cells (Lavie et al., 2001). Lung cancer is the most frequent cause of cancer-related death, in part because of its propensity to metastasize before the cancer is diagnosed. Using a human lung cancer cell line, α-chaconine was shown to reduce metastasis and it was suggested this may allow new chemotherapeutic approaches (Shih et al., 2007).

A separate study showed that solamargine, a glycoalkaloid found in some potatoes, increased the susceptibility of two different types of human lung cancer cell lines to several anticancer drugs (Liang et al., 2008). Beyond potential anticancer efficacy, GAs have been shown to boost the immune response. Mice fed GAs were more resistance to infection by *Salmonella* (Gubarev et al., 1998) and tomatine was demonstrated to potentiate the mice immune response to vaccines (Rajananthanan et al., 1999). GAs are reported to inactivate several types of herpes viruses (Chataing et al., 1997).

Much more medical information about the bioavailability, dietary relevance and both positive and negative effects on health of individual GAs must be obtained before it will be possible to develop potatoes with an optimal GA compliment.

14.9 Potato Minerals

A wide range of mineral elements occurs in fruits and vegetables, which are a primary dietary source. Minerals can generally be classified as major minerals such as calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), phosphorus (P), cobalt (Co), manganese (Mn), nitrogen (N), chlorine (Cl), and nutritionally essential minor and trace minerals such as iron (Fe), copper (Cu), selenium (Se), Nickel (Ni), lead (Pb), sulfur (S), boron (B), iodine (I), silicon (Si), bromine (Br). The importance of optimal mineral intake to maintain good health is widely recognized (Avioli, 1998).

Potatoes are an important source of different dietary minerals. Potato is listed as providing 18% of the RDA of potassium, 6% of iron, phosphorus and magnesium, and 2% calcium and zinc. Retention of most minerals is high in boiled potatoes cooked with skin (True et al., 1979). Baking a potato with the skin is a good cooking method to retain minerals.

There are significant differences in major and trace mineral contents amongst different genotypes of potato (Randhawa et al., 1984; True et al., 1978). Potassium levels varied the most and manganese the least. In a study of 74 Andean landraces, the iron content ranged from 29.87 to 157.96 μg/DW, the zinc content from 12.6 to 28.83 μg/g DW, and the calcium content from 271.09 to 1092.93 μg/g DW (Andre et al., 2007).

Many factors affect the mineral composition of potatoes, for example location, stage of development, soil type, soil pH, soil organic matter, fertilization, irrigation, and weather. Genotypic variation is also important. Cationic mineral content in *Arabidopsis* is genetically controlled and candidate genes identified are cation transporters (Vreugdenhil, 2004). The same genotypes grown in different locations may have different mineral concentration due to environmental interactions (Burgos et al., 2007).

Potassium, phosphorus, calcium, and magnesium concentrations changed with irrigation and fertilization in physiologically mature tubers (Ilin et al., 2002). The total concentration of iron, calcium, and zinc increased with application of fertilizers whereas the content of phosphorus and molybdenum was reduced (Bibak et al., 1999; Frossard et al., 2000). The wide range of mineral content reported in potatoes may not only be due to genotype and environmental factors, but also sampling issues.

14.9.1 Potassium

In terms of mineral content, potato is best known as an important source of dietary potassium, which plays a fundamental role in acid–base regulation and fluid balance and is required for optimal functioning of the heart, kidneys, muscles, nerves, and digestive systems. Health benefits of sufficient potassium intake include reduced risk of hypokalemia, osteoporosis, high blood pressure, stroke, inflammatory bowel disease (IBD), kidney stones, and asthma. A high intake of potassium and low intake of sodium have been hypothesized to reduce the risk of stroke (Larsson et al., 2008; Swain et al., 2008). However, most American women 31–50 years old consume no more than half of the recommended amount of potassium and men's intake is only moderately higher (IOM, 2004).

Potatoes qualify for a health claim approved by the U.S. Food and Drug Administration, which states: 'Diets containing foods that are good source of potassium and that are low in sodium may reduce the risk of high blood pressure and stroke.' Potatoes rank highest for potassium content among 20 most frequently consumed raw vegetables and fruits (source: US Potato Board; DHHS FDA). Potassium varies from 3550–8234 μg/g FW (Casañas et al., 2002; Rivero et al., 2003; Sánchez-Castillo, 1998). One report listed potassium as low as 5.6 μg/g FW (True et al., 1978). Potassium content increases during the entire growing season (Lisinka and Leszczynski, 1989). On average one baked potato (156 g) contains 610 mg potassium (USDA/HHS, 2005). This is an even higher amount than in banana, a food often recommended by dieticians to people who need to supplement potassium consumption. The dietary reference intake of potassium for adult men and women is 3000–6000 mg per day. The US National Academy of Sciences recently increased the recommended intake for potassium from 3500 mg to at least 4700 mg per day.

14.9.2 Phosphorus

Besides potassium, phosphorus is the main mineral present in the tubers. It has many roles in the human body and is a key player for healthy cells, teeth, and bones. Inadequate phosphorus intake results in abnormally low serum phosphate levels, which affect loss of appetite, anemia, muscle weakness, bone pain, rickets osteomalacia, susceptibility to infection, numbness and tingling of the extremities, and difficulty walking. In potatoes phosphorus ranges from ~1300–6000 μg/g DW (Lisinka and Leszczynski, 1989; Randhawa, 1984; Sánchez-Castillo, 1998). Daily requirements are 800–1000 mg.

14.9.3 Calcium

Potatoes are a significant source of calcium, with a wide range reported. Two studies reported calcium content up to 130 mg/100 g DW and 455 mg/kg FW (Lisinka and Leszczynski, 1989; Randhawa, 1984). Among 74 Andean landraces, calcium ranged from 271–1093 μg/g DW (Andre et al., 2007a). Wild *Solanum* species vary in the ability to accumulate tuber calcium (Bamberg, 1998). High levels of tuber calcium are associated with resistance to pathogens (McGuire, 1986) and abiotic stress (Tawfik, 1996). Calcium is important for bone and tooth structure, blood clotting, and nerve transmission. Deficiencies are associated with skeletal malformations and blood pressure abnormalities. The RDA for calcium is set at levels to reduce osteoporosis (Bachrach, 2001; Bryant et al., 1999) and varies depending on age and gender, but for young adults is 1300 mg.

14.9.4 Magnesium

Potato magnesium levels range from 142 to 359 μg/g FW (Casañas et al., 2002; Rivero et al., 2003). Magnesium is required for normal functioning of muscles, heart, and immune system. Magnesium also helps maintain normal blood sugar levels and blood pressure. The RDA for magnesium is 400–600 mg.

14.9.5 Manganese

The range of potato manganese content has been reported from 0.73–3.62 μg/g FW (Rivero et al., 2003) to 9–13 μg/g DW (Orphanos, 1980). Manganese has a role in blood sugar regulation, metabolism, and thyroid hormone function. Recommended daily intake in the USA is 2–10 mg.

14.9.6 Iron

Iron deficiency affects more than 1.7 billion people worldwide and has been called the most widespread health problem in the world by the World Health Organization. Due to severe iron deficiency, more than 60 000 women die in pregnancy and childbirth each year, and almost 500 million women of childbearing age suffer from anemia. Dietary iron requirements depend on numerous factors, for example, age, sex, and diet composition. Recommended daily intake in the USA varies dependent on gender and age. Potato is a modest source of iron. A study of cultivated varieties showed 0.3–2.3 mg of Fe in a 100 g tuber (True et al., 1978). Ranges of iron content from 6 to 158 μg/g of DW have been reported (Andre et al., 2007; Wills et al., 1984). Some Andean potatoes have iron content comparable to levels found in some cereals (rice, maize, and wheat; Scurrah et al., 2007). Potato iron should be quite bioavailable because it has very low levels of phytic acid, unlike the cereals.

14.9.7 Zinc

Significant differences in zinc content occur in potatoes. The zinc content ranges from 1.8 to 10.2 μg/g FW (Andre et al., 2007; Randhawa et al., 1984; Rivero et al., 2003). Yellow-fleshed potatoes from different cultivars contain zinc in 0.5–4.6 μg/g FW (Dugo et al., 2004). Zinc is needed for the body's immune system to properly work and is involved in cell division, cell growth, and wound healing. The US RDA is 15–20 mg.

14.9.8 Copper

Copper in potatoes varies from 0.23 to 11.9 mg/kg FW (Randhawa et al., 1984; Rivero et al., 2003). Like zinc, copper is also high in yellow-fleshed potatoes (Dugo et al., 2004). Copper is needed for synthesis of hemoglobin, proper iron metabolism, and maintenance of blood vessels. The US RDA is 1.5–3.0 mg.

14.10 Potato phenolics

Potatoes are an important source of dietary phenolics. Phenolics are a diverse group of tens of thousands of different compounds, some of which are effective against diseases or have other health-promoting qualities including effects on longevity, mental acuity, cardiovascular disease, and eye health (Manach et al., 2004; Parr and Bolwell, 2000; Scalbert et al., 2005). Phenolics are the most abundant antioxidants in the diet. Plant phenolics may contain a treasure trove of potential health-promoting compounds. For example, many of the reports in the popular press about positive health effects of green tea, coffee, or wine are due to phenolic content. The role of phenolics in health is an area of active ongoing medical research that is only beginning to be understood. Upon consumption, phenolics are metabolized by digestive and hepatic enzymes, by the intestinal microflora and have a wide range of bioavailability not yet thoroughly defined (Manach et al., 2004). Conducting a Google search using phenolics and health as keywords returned over 700 000 links in 2005 and 1.6 million in 2008, reflecting the rising interest in these phytonutrients.

A study of 74 Andean potato landraces found about an 11-fold variation in total phenolics and a high correlation between phenolics and total antioxidant capacity (Andre et al., 2007a). We screened tubers from hundreds of cultivars and wild potato species for phenolics and found over a 15-fold difference in the amount of phenolics in different potato genotypes. Many phenolics are colorless, and thus are relevant phytonutrients for white-fleshed cultivars, which are the consumer-preferred type of potato in many countries. Russet Norkotah has high amounts among the white-fleshed cultivars, about 4 mg/g DW. *S. Pinnatisectum*, a purple-fleshed wild species,

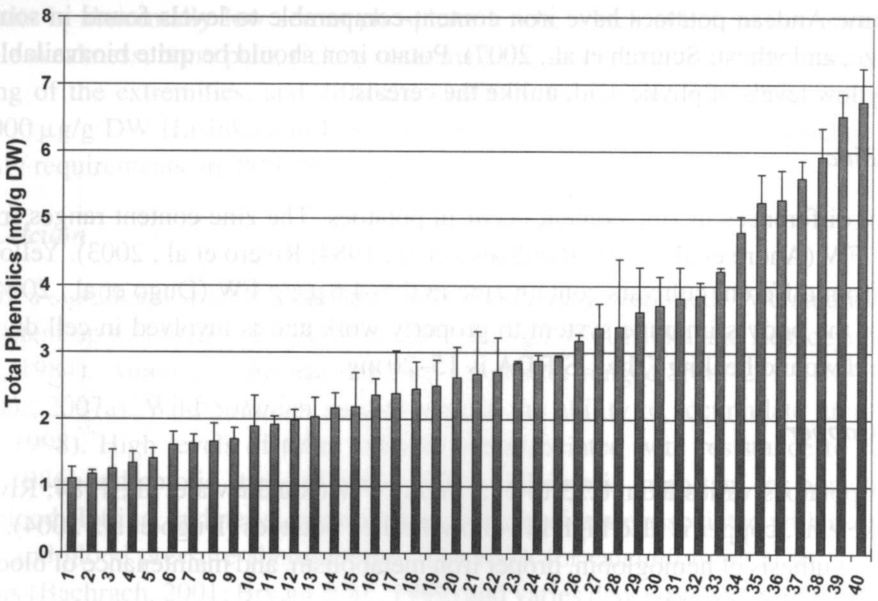


Figure 14.4: The wide range of total phenolics possible in potato tubers is evident in this analysis of 40 genotypes. LCMS analysis was used to obtain phenolic profiles from tuber extracts. Total phenolics of three independent replicates are shown with standard deviation.

has over 5 mg/g DW total phenolics. The potatoes with the highest total phenolics we have yet found are purple-fleshed lines, such as the two genotypes shown in Figure 14.4 with over 6.5 mg/g DW total phenolics.

If we compare high phenolic potatoes to some published reports of total phenolic amounts found in other plants, these potatoes have more phenolics than tomatoes, peas, onions, French beans, cucumbers, white cabbage, carrots, lettuce, or cucumbers (Figure 14.5). Furthermore, the amounts in these potatoes rival some reported phenolic amounts for broccoli, Brussels sprouts, and spinach. We have identified several potato genotypes that have over double the phenolic amounts of the potatoes listed in Figures 14.4 and 14.5. Thus, potatoes can be a substantial source of phenolics in the diet and compare very favorably to other vegetables. One study evaluated the contribution of 34 fruits and vegetables to phenolic intake in the American diet and concluded that potatoes were the third most important source after apples and oranges (Chun et al., 2005). The potatoes used in this study were an unspecified variety bought at a supermarket and almost certainly contained a small amount of phenolics relative to the high phenolic potatoes. The variation in phenolic content in potatoes is an excellent example of the potential to further increase its nutritional value by more fully utilizing existing germplasm.

Many potato nutrients differ in the amounts that accumulate in the skin versus the flesh. The majority of phenolic compounds are found in greater concentrations in the skin, but large

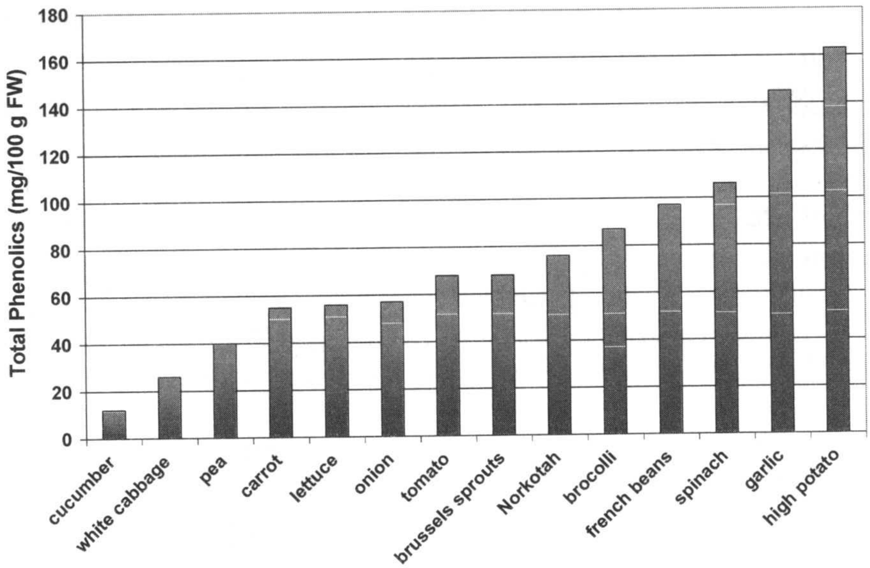


Figure 14.5: Total phenolic content of multiple vegetables is shown. Russet Norkotah and an advanced breeding line labeled 'high potato' are the two potato types used in this comparison.

quantities are also present in the flesh. Because a sizeable majority of the fresh weight of a mature potato is contributed by the flesh, overall the flesh will typically contain more phenolics than the skin on a per tuber basis. Potato skins are well known to be nutritious and consumers who realize this can choose recipes and products which include skins. Since potato skins are a rich source of phenolics (Nara et al., 2006), the phenolic content in the potato skins generated as waste during French fry processing might be easily recoverable and a potential 'value-added' product.

14.10.1 Chlorogenic acid

The most abundant phenolics in tubers are caffeoyl-esters. Typically chlorogenic acid (CGA; Figure 14.6) comprises over 90% of a tuber's total phenolics (Malmberg and Theander, 1985). Given the enormous contribution of CGA to the total phenolic content of potatoes, an interesting question is what changes in the tuber phenolic complement would occur if CGA formation was inhibited by antisense or RNAi methods. The biosynthetic pathway of chlorogenic acid in plants has been elucidated, creating new opportunities for engineering CGA biosynthesis in potatoes (Niggeweg et al., 2004).

There is evidence that chlorogenic acid has numerous health-promoting effects and CGA supplements are available in health stores. Dietary CGA is bioavailable in humans (Monteiro et al., 2007), is known to protect animals against degenerative, age-related diseases when added to

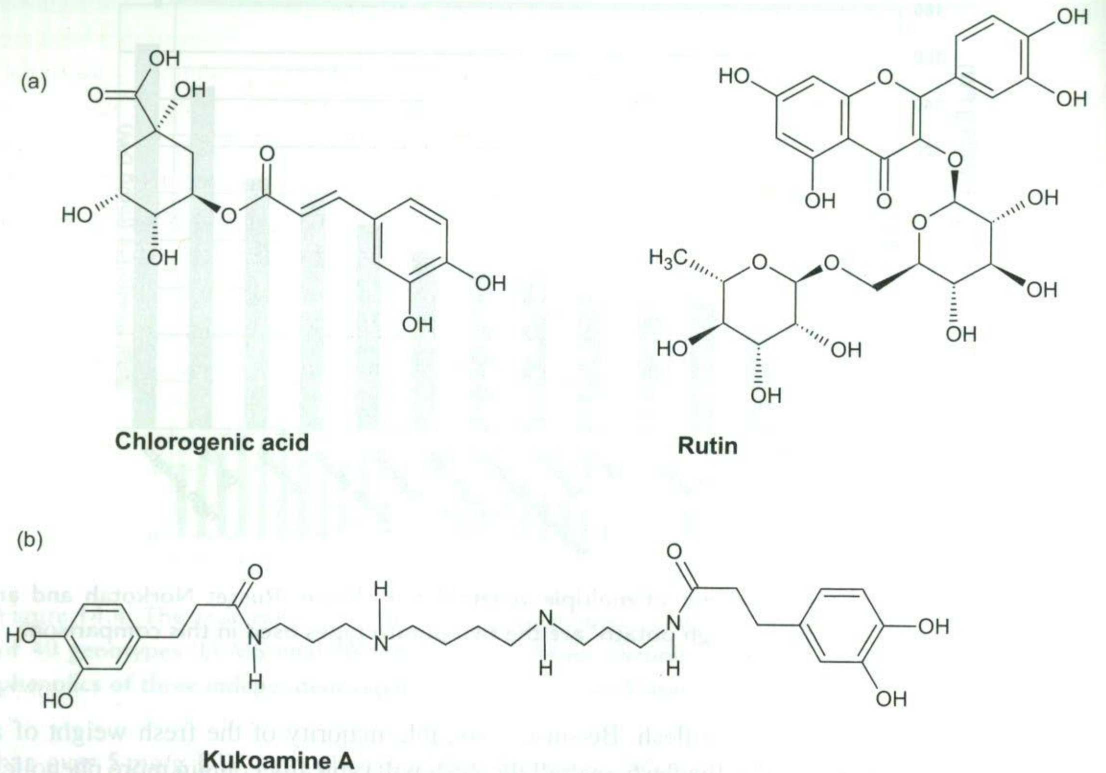


Figure 14.6: Structure of chlorogenic acid, rutin and kukoamine A.

their diet, and may reduce the risk of some cancers and heart disease (Nogueira and do Lago, 2007). CGA is also thought to be anti-hypertensive (Yamaguchi et al., 2007). CGA is reported to be anti-viral and anti-bacterial. Chlorogenic acid may decrease the risk of type 2 diabetes (Legrand and Scheen, 2007) and has been shown to slow the release of glucose into the bloodstream (Bassoli et al., 2008). This could be important towards lowering the glycemic index value of potatoes.

A concern about developing high phenolic potatoes is whether they would have unacceptable levels of browning or after cooking darkening, as suggested by the older literature. One more recent study showed that neither the amount of total phenolics, chlorogenic acid, or polyphenol oxidase correlated with the amount of browning observed in fresh-cut potatoes and that they were not rate-limiting in the development of browning (Cantos et al., 2002). Additionally, using a QTL approach, another group found no correlation between browning and chlorogenic acid (Werij et al., 2007).

14.11 Flavonols, anthocyanins, and kukoamines

Potatoes contain flavonols such as rutin (Figure 14.6), but have not been thought to be important sources of dietary flavonols, however little is known about qualitative and quantitative variation of flavonols in diverse germplasm. One group showed that flavonols increased in fresh-cut tubers, observing concentrations up to 14 mg/100 g FW and suggested that because of the large amount of potatoes consumed, they can be a valuable dietary source (Tudela et al., 2002a). In our screening of potato germplasm we have found over a 30-fold difference in flavonol content. Numerous studies suggest quercetin and related flavonols have multiple health-promoting effects, including reduced risk of heart disease, lowered risk of certain respiratory diseases, such as asthma, bronchitis, and emphysema, and reduced risk of some cancers including prostate and lung cancer.

Potatoes, particularly colored-fleshed cultivars, can contain substantial amounts of anthocyanins, compounds that can function as antioxidants and have other health-promoting effects. A gene encoding dihydroflavonol 4-reductase is required for production of pelargonidins in potato and other candidate genes have been identified (De Jong et al., 2003, 2004). A recent report found that an anthocyanin-enriched fraction from potatoes had anticancer properties (Reddivari et al., 2007). Lewis et al. (1998) screened 26 colored-fleshed cultivars for anthocyanin content and found up to 7 mg/g FW in the skin and 2 mg/g FW in the flesh. Another study evaluated 31 colored genotypes and found a range of 0.5 to 3 mg/g FW in the skin and up to 1 mg/g FW in the flesh (Jansen and Flamme, 2006). Brown et al. (2005) evaluated several genotypes for anthocyanins and found whole tubers that contained up to 4 mg/g FW and that anthocyanin concentration correlated with antioxidant value.

In June 2005, a British group reported the discovery of compounds called kukoamines in potatoes (Parr et al., 2005). These compounds are phenolic–polyamine conjugates (Figure 14.6) and had previously only been found in a Chinese medicinal plant, in which they were being studied because they lower blood pressure. It still needs to be established whether enough of these compounds survive cooking and are bioavailable enough to have any effect on humans. Nevertheless, the presence of these compounds is indicative of the complex chemical makeup of tubers. In our LCMS analysis of tubers, we have observed up to 30 putative polyamines in a single tuber. Roles for tuber polyamines include regulation of starch biosynthesis (Tanemura and Yoshino, 2006), calystegine synthesis (Stenzel et al., 2006), disease resistance (Matsuda et al., 2005), and sprouting (Kaur-Sawhney et al., 1982).

14.12 Carotenoids

Most of the compounds described to this point are hydrophilic. Potatoes also contain lipophilic compounds that are dietarily desirable, such as carotenoids. Carotenoids are synthesized in plastids from isoprenoids (Dellapenna and Pogson, 2006) and one role is coping with photo- and oxidative stress. Over a 20-fold range in carotenoid concentrations has been reported in potato germplasm with much of the variation controlled at the transcriptional level (Morris et al., 2004).

Carotenoids have numerous health-promoting properties including provitamin A activity and decreased risk of several diseases (Fraser and Bramley, 2004). Because two of the most abundant potato carotenoids are lutein and zeaxanthin, potatoes may be particularly important for eye health and reduced risk of age-related macular degeneration (Chucair et al., 2007; Tan et al., 2008). The carotenoid complement varies by cultivar, but violaxanthin and lutein are usually the most abundant tuber carotenoids. The yellow/orange flesh color found in some potatoes is due to carotenoids. Orange coloration in potatoes is due to zeaxanthin (Brown et al., 1993) whereas the lutein concentration correlates well with the intensity of yellow coloration. White-fleshed potatoes usually contain less carotenoids than the yellow or orange cultivars. One study found white cultivars had 27–74 μg/100g FW of carotenoids (Iwanzik et al., 1983). Cultivated diploid potatoes derived from *S. stenotomum* and *S. phureja* were found to contain up to 2000 μg/100 g FW of zeaxanthin (Brown et al., 1993). A study of 74 Andean landraces found total carotenoids concentrations ranging from 3 to 36 μg/g DW (Andre et al., 2007a). A screen of 24 Andean cultivars identified genotypes with almost 18 μg/g DW each of lutein and zeaxanthin and just over 2 μg/g DW of β-carotene (Andre et al., 2007b).

Numerous groups recently have attempted to increase potato carotenoids using transgenic strategies. Overexpressing a bacterial phytoene synthase in tubers of the cultivar Desiree increased carotenoids from 5.6 to 35 μg/g DW and changed the ratios of individual carotenoids. β-carotene concentrations increased from trace amounts to 11 μg/g DW and lutein levels increased 19-fold (Ducreux et al., 2005). Carotenoids can be increased by approaches that do not directly involve use of carotenoid biosynthesis genes, as shown by overexpression of the cauliflower Or gene in Desiree resulting in a six-fold increase in tuber carotenoids to about 20–25 μg/g DW (Lu et al., 2006). A two-fold increase in carotenoids was observed in tubers overexpressing Or after 6 months of cold storage but no such increase was observed in wild-type or empty-vector transformed plants (Lopez et al., 2008). This is in contrast to what is seen with cultivars undergoing cold storage that undergo a decline in total carotenoids during storage (Griffiths et al., 2007; Morris et al., 2004).

An elegant approach using three bacterial genes overexpressed in Desiree achieved a 20-fold increase in total carotenoids to 114 μg/G DW and a 3600-fold increase in B-carotene to 47 μg/g DW (Diretto et al., 2007). A 250 g serving of these potatoes was estimated to provide 50% of the RDA of vitamin A. Potatoes engineered to have higher zeaxanthin levels were fed to human subjects and the zeaxanthin was found to be readily bioavailable (Bub et al., 2008).

14.13 Conclusion

Although this chapter is by no means a comprehensive listing of all health-promoting compounds present in tubers, it does give a good sense of the complexity of tuber chemistry and how the starch content of the tuber is only a small part of the story. The diverse milieu of tuber metabolites may be partly a reflection of the complexity of a tuber's primary task: to allow the plant to survive in varied environments.

Efforts to maximize the nutritional potential of potatoes are in their very early stages. Given the genetic diversity of wild-potato species available to be tapped into for nutritionally superior traits and the ever-increasing power of biotech approaches it is clear that future cultivars have the potential to be nutritional powerhouses.

References

Alfthan, G., Laurinen, M. S., Valsta, L. M., Pastinen, T., & Aro, A. (2003). Folate intake, plasma folate and homocysteine status in a random Finnish population. *Eur. J. Clin. Nutr.*, *57*, 81–88.

Andre, C. M., Ghislain, M., Bertin, P., Oufir, M., Herrera Mdel, R., Hoffmann, L., Hausman, J. F., Larondelle, Y., & Evers, D. (2007a). Andean potato cultivars (Solanum tuberosum L.) as a source of antioxidant and mineral micronutrients. *J. Agric. Food Chem.*, *55*, 366–378.

Andre, C. M., Oufir, M., Guignard, C., Hoffmann, L., Hausman, J. F., Evers, D., & Larondelle, Y. (2007b). Antioxidant profiling of native Andean potato tubers (Solanum tuberosum L.) reveals cultivars with high levels of beta-carotene, alpha-tocopherol, chlorogenic acid, and petanin. *J. Agric. Food Chem.*, *55*, 10839–10849.

Arnqvist, L., Dutta, P. C., Jonsson, L., & Sitbon, F. (2003). Reduction of cholesterol and glycoalkaloid levels in transgenic potato plants by overexpression of a type 1 sterol methyltransferase cDNA. *Plant Physiology*, *131*(4), 1792–1799.

Augustin, J., Johnson, S. R., Teitzel, C., True, R. H., Hogan, J. M., Toma, R. B., Shaw, R. L., & Deutsch, R. M. (1978a). Changes in the nutrient composition of potatoes during home preparation II. *American Potato Journal*, *55*, 653–662.

Augustin, J., Johnson, S. R., Teitzel, C., Toma, R. B., Shaw, R. L., True, R. H., Hogan, J. M., & Deutsch, R. M. (1978). Vitamin composition of freshly harvested and stored potatoes. *Journal of Food Science*, *43*, 1566–1570, 1574.

Augustin, J., Marousek, G. I., Tholen, L. A., & Bertelli, B. (1980). Vitamin retention in cooked, chilled, and reheated potatoes. *Journal of Food Science*, *45*, 814–816.

Augustin, J., Toma, R. B., True, R. H., Shaw, R. L., Teitzel, C., Johnson, S. R., & Orr, P. (1979). Composition of raw and cooked potato peel and flesh: proximate and vitamin composition. *J. Food Sci.*, *44*, 805.

Bachrach, L. K. (2001). Acquisition of optimal bone mass in childhood and adolescence. *Trends Endocrin. Met.*, *12*, 22–28.

Bailey, L. B., Rampersaud, G. C., & Kauwell, G. P. (2003). Folic acid supplements and fortification affect the risk for neural tube defects, vascular disease and cancer: evolving science. *J. Nutr.*, *133*, 1961S–1968S.

Basset, G. J. C., Quinlivan, E. P., Gregory, J. F., & Hanson, A. D. (2005). Folate synthesis and metabolism in plants and prospects for biofortification. *Crop. Sci.*, *45*, 449–453.

Bassoli, B. K., Cassolla, P., Borba-Murad, G. R., Constantin, J., Salgueiro-Pagadigorria, C. L., Bazotte, R. B., da Silva, R. S., & de Souza, H. M. (2008). Chlorogenic acid reduces the plasma glucose peak in the oral glucose tolerance test: effects on hepatic glucose release and glycaemia. *Cell Biochem. Funct.*, *26*, 320–328.

Bekaert, S., Storozhenko, S., Mehrshahi, P., Bennett, M. J., Lambert, W., Gregory, J. F. 3rd, Schubert, K., Hugenholtz, J., Van Der Straeten, D., & Hanson, A. D. (2007). Folate biofortification in food plants. *Trends Plant Sci.*, *13*, 28–35.

Bibak, A., Sturup, S., Haahr, V., Gundersen, P., & Gundersen, V. (1999). Concentrations of 50 major and trace elements in Danish agricultural crops measured by inductively coupled plasma mass spectrometry. 3. Potato (Solanum tuberosum Folva). *J. Agric. Food Chem.*, *47*, 2678–2684.

Brevik, A., Vollset, S. E., Tell, G. S., Refsum, H., Ueland, P. M., Loeken, E. B., Drevon, C. A., & Andersen, L. F. (2005). Plasma concentration of folate as a biomarker for the intake of fruit and vegetables: the Hordaland Homocysteine Study. *Am. J. Clin. Nutr.*, *81*, 434–439.

Brown, C. R., Culley, D., Yang, C., Durst, R., & Wrolstad, R. (2005). Variation of anthocyanin and carotenoid contents and associated antioxidant values in potato breeding lines. *J. Amer. Soc. Hort. Sci.*, *130*, 174–180.

Brown, C. R., Edwards, C. G., Yang, C. P., & Dean, B. B. (1993). Orange flesh trait in potato: inheritance and carotenoid content. *Journal of the American Society for Horticultural Science*, *118*, 145–150.

Brussaard, J. H., Löwik, M. R., van den Berg, H., Brants, H. A., & Goldbohm, R. A. (1997). Folate intake and status among adults in the Netherlands. *Eur. J. Clin. Nutr.*, *51*(Suppl 3), S46–50.

Bryant, R. J., Cadogan, J., & Weaver, C. M. (1999). The new dietary reference intakes for calcium: Implications for osteoporosis. *J. Coll. Nutr.*, *18*, 406S–412S.

Bub, A. M. D., Möseneder, J., Wenzel, G., Rechkemmer, G., & Briviba, K. (2008). Zeaxanthin is bioavailable from genetically modified zeaxanthin-rich potatoes. *European Journal of Nutrition*, *47*(2), 99–103.

Burgos, G., Amoros, W., Marote, M., Stangoulis, J., & Bonierbale, M. (2007). Iron and zinc concentration of native potato cultivars from a human nutrition perspective. *J. Sci. Food Agric.*, *87*, 668–675.

Cantos, E., Tudela, J. A., Gil, M. I., & Espin, J. C. (2002). Phenolic compounds and related enzymes are not rate-limiting in browning development of fresh-cut potatoes. *Journal of Agricultural and Food Chemistry*, *50*, 3015–3023.

Casañas, R., González, M., Rodríguez, E., Morrero, A., & Diaz, C. (2002). Chemometric studies of chemical compounds in five cultivars of potatoes from Tenerife. *J. Agric. Food Chem.*, *50*, 2076–2082.

Cham, B. E. (1994). Solasodine glycosides as anti-cancer agents: pre-clinical and clinical studies. *S. Asia Pacific Journal of Pharmacology*, *9*, 113–118.

Chataing, B., Concepcion, J. L., de Cristancho, N. B., & Usubillaga, A. (1997). Estudio clinico de la efectividad de extractos alcaloides obtenidos de los frutos del Solanum americanum Miller sobre el Herpes simplex, Herpes Zoster y Herpes genitalis. *Revista de la Facultad de Farmacia*, *32*, 18–25.

Chucair, A. J., Rotstein, N. P., Sangiovanni, J. P., During, A., Chew, E. Y., & Politi, L. E. (2007). Lutein and zeaxanthin protect photoreceptors from apoptosis induced by oxidative stress: relation with docosahexaenoic acid. *Invest. Ophthalmol Vis. Sci.*, *48*, 5168–5177.

Chun, O. K., Kim, D. O., Smith, N., Schroeder, D., Han, J. T., & Lee, C. Y. (2005). Daily consumption of phenolics and total antioxidant capacity from fruit and vegetables in the American diet. *Journal of the Science of Food and Agriculture*, *85*(10), 1715–1724.

Dale, M. F. B., Griffiths, D. W., & Todd, D. T. (2003). Effects of genotype, environment, and postharvest storage on the total ascorbate content of potato (Solanum tuberosum) tubers. *J. Agric. Food Chem.*, *51*, 244–248.

De Jong, W. S., De Jong, D. M., De Jong, H., Kalazich, J., & Bodis, M. (2003). An allele of dihydroflavonol 4-reductase associated with the ability to produce red anthocyanin pigments in potato (Solanum tuberosum L.). *Theoretical and Applied Genetics*, *107*(8), 1375–1383.

De Jong, W. S., Eannetta, N. T., De Jong, D. M., & Bodis, M. (2004). Candidate gene analysis of anthocyanin pigmentation loci in the Solanaceae. *Theoretical and Applied Genetics*, *108*(3), 423–432.

de la Garza, R., Quinlivan, E. P., Klaus, S. M., Basset, G. J., Gregory, J. F. 3rd, & Hanson, A. D. (2004). Folate biofortification in tomatoes by engineering the pteridine branch of folate synthesis. *Proc. Natl. Acad. Sci. U. S. A.*, *101*, 13720–13725.

Dellapenna, D., & Pogson, B. (2006). Vitamin Synthesis in Plants: Tocopherols and Carotenoids. *Annu. Rev. Plant Biol.*, *57*, 711–738.

Deng, X. W., & Gruissem, W. (1988). Constitutive transcription and regulation of gene expression in non-photosynthetic plastids of higher plants. *Embo. J.*, *7*, 3301–3308.

Denslow, S. A., Walls, A. A., & Daub, M. E. (2005). Regulation of biosynthetic genes and antioxidant properties of vitamin B b6 s vitamers during plant defense responses. *Physiological and Molecular Plant Pathology*, *66*(6), 244–255.

Díaz de la Garza, R. I., Gregory, J. F. 3rd, & Hanson, A. D. (2007). Folate biofortification of tomato fruit. *Proc. Natl. Acad. Sci. USA*, *104*, 4218–4222.

Diretto, G., Al-Babili, S., Tavazza, R., Papacchioli, V., Beyer, P., & Giuliano, G. (2007). Metabolic engineering of potato carotenoid content through tuber-specific overexpression of a bacterial mini-pathway. *PLoS ONE*, *2*, e350.

Ducreux, L. J. M., Morris, W. L., Hedley, P. E., Shepherd, T., Davies, H. V., Millam, S., & Taylor, M. A. (2005). Metabolic engineering of high carotenoid potato tubers containing enhanced levels of beta-carotene and lutein. *Journal of Experimental Botany*, *56*(409), 81–89.

Dugo, G., La Pera, L., Lo Turco, V., Giuffrida, D., & Restuccia, S. (2004). Determination of copper, zinc, selenium, lead and cadmium in potatoes (Solanum tubersom L.) using potentiometric stripping methods. *Food Addit. Contam.*, *2*(7), 649–657.

Ewing, E. E., & Struik, P. C. (1992). Tuber formation in potato: induction, initiation, and growth. *Horticultural Reviews*, *14*, 89–198.

Fernie, A. R., & Willmitzer, L. (2001). Molecular and biochemical triggers of potato tuber development. *Plant Physiology*, *127*, 1459–1465.

Finglas, P. M., de Meer, K., Mollo, y. A., Verhoef, P., Pietrzik, K., Powers, H. J., van der Straeten, D., Jägerstad, M., Varela-Moreiras, G., van Vliet, T., Havenaar, R., Buttriss, J., & Wright, A. J. (2006). Research goals for folate and related B vitamin in Europe. *Eur. J. Clin. Nutr.*, *60*, 287–294.

Flamini, R. (2003). Mass spectrometry in grape and wine chemistry. Part I: polyphenols. *Mass Spectrom. Rev.*, *22*, 218–250.

Forssén, K. M., Jägerstad, M. I., Wigertz, K., & Witthöft, C. M. (2000). Folates and dairy products: a critical update. *J. Am. Coll. Nutr.*, *19*, 100S–110S.

Fraser, P. D., & Bramley, P. M. (2004). The biosynthesis and nutritional uses of carotenoids. *Prog. Lipid Res.*, *43*, 228–265.

Freisleben, A., Schieberle, P., & Rychlik, M. (2003 May). Specific and sensitive quantification of folate vitamers in foods by stable isotope dilution assays using high-performance liquid chromatography-tandem mass spectrometry. *Anal. Bioanal. Chem.*, *376*(2), 149–156.

Friedman, M. (2002). Tomato glycoalkaloids: role in the plant and in the diet. *J. Agric. Food Chem.*, *50*, 5751–5780.

Friedman, M. (2006). Potato glycoalkaloids and metabolites: roles in the plant and in the diet. *J. Agric. Food Chem.*, *54*, 8655–8681.

Friedman, M., Lee, K. R., Kim, H. J., Lee, I. S., & Kozukue, N. (2005). Anticarcinogenic effects of glycoalkaloids from potatoes against human cervical, liver, lymphoma, and stomach cancer cells. *J. Agric. Food Chem.*, *53*, 6162–6169.

Friedman, M., & McDonald, G. M. (1997). Potato glycoalkaloids: chemistry, analysis, safety, and plant physiology. *Critical Reviews in Plant Sciences*, *16*(1), 55–132.

Friedman, M., McQuistan, T., Hendricks, J. D., Pereira, C., & Bailey, G. S. (2007). Protective effect of dietary tomatine against dibenzo[a,l]pyrene (DBP)-induced liver and stomach tumors in rainbow trout. *Mol. Nutr. Food Res.*, *51*, 1485–1491.

Frossard, E., Bucher, E., Machler, E., Mozafar, A., & Hurrell, R. (2000). Potential for increasing the content and bioavailability of Fe, Zn and Ca in the plants for human nutrition. *J. Sci. Food Agric.*, *80*, 861–879.

Gibson, R. S., Perlas, L., & Hotz, C. (2006). Improving the bioavailability of nutrients in plant foods at the household level. *Proc. Nutr. Soc.*, *65*, 160–168.

Goyer, A., & Navarre, D. A. (2007). Determination of folate concentrations in diverse potato germplasm using a trienzyme extraction and a microbiological assay. *J. Agric. Food Chem.*, *55*, 3523–3528.

Griffiths, D. W., Bain, H., & Dale, M. F. B. (1997). The effect of low-temperature storage on the glycoalkaloid content of potato (Solanum tuberosum) tubers. *Journal of the Science of Food and Agriculture*, *74*, 301–307.

Griffiths, D. W., Dale, M. F., Morris, W. L., & Ramsay, G. (2007). Effects of season and postharvest storage on the carotenoid content of Solanum phureja potato tubers. *J. Agric. Food Chem.*, *55*, 379–385.

Gubarev, M. I., Enioutina, E. Y., Taylor, J. L., Visic, D. M., & Daynes, R. A. (1998). Plant derived glycoalkaloids protect mice against lethal infection with Salmonella typhimurium. *Phytotherapy Research: PTR*, *12*, 79–88.

Han, J. Y., & Tyler, R. T. (2003). Determination of folate concentrations in pulses by a microbiological method employing trienzyme extraction. *J. Agric. Food Chem.*, *51*, 5315–5318.

Hatzis, C. M., Bertsias, G. K., Linardakis, M., Scott, J. M., & Kafatos, A. G. (2006). Dietary and other lifestyle correlates of serum folate concentrations in a healthy adult population in Crete, Greece: a cross-sectionial study. *Nutr. J.*, *5*, 5.

Hawkes, J. G. (1990). *The potato evolution, biodiversity & genetic resources*. Smithsonian Institution Press, Washington, D.C.

Heftmann, E. (1983). Biogenesis of steroids in Solanaceae. *Phytochemistry*, *22*(9), 1843–1860.

Holland, B., Unwin, I. D., & Buss, D. H. (1996). *Vegetables, Herbs and Spices. Fruits and Nuts*. Royal Society of Chemistry, Cambridge, UK.

Hopkins, J. (1995). The glycoalkaloids: naturally of interest (but a hot potato?). *Food Chem. Toxicol.*, *33*, 323–328.

Ilin, Z., Durovka, M. and Markovic, V. (2002). Effect of irrigation and mineral nutrition on the quality of potato. In: Balkan symposium on vegetables and potatoes.

Institute of Medicine (IOM), (2004). Dietary Reference Intakes: Water, potassium, sodium chloride, and sulfate. National Academy Press, Washington.

Iwanzik, W., Tevini, M., Stute, R., & Hilbert, R. (1983). Carotinoidgehalt und -zusammensetzung verschiedener deutscher Kartoffelsorten und deren Bedeutung fur die Fleischfarbe der Knolle. *Potato Research*, *26*, 149–162.

Jackson, S. D. (1999). Multiple signaling pathways control tuber induction in potato. *Plant Physiol.*, *119*, 1–8.

Jansen, G., & Flamme, W. (2006). Coloured potatoes (Solanum Tuberosum L.) - Anthocyanin Content and Tuber Quality. *Genetic Resources and Crop Evolution*, *53*(7), 1321–1331.

Johnson, D. F., Bennett, R. D., & Heftmann, E. (1963). Cholesterol in higher plants. *Science*, *140*, 198–199.

Jones, M. L., & Nixon, P. F. (2002). Tetrahydrofolates are greatly stabilized by binding to bovine milk folate-binding protein. *J. Nutr.*, *132*, 2690–2694.

Kaneko, K., Tanaka, M. W., & Mitsuhashi, H. (1976). Origin of nitrogen in the biosynthesis of solanidine by Veratrum grandiflorum. *Phytochemistry*, 1391–1393.

Kant, A. K., & Block, G. (1990). Dietary vitamin B-6 intake and food sources in the US population: NHANES II, 1976-1980. *Am. J. Clin. Nutr.*, *52*, 707–716.

Kariluoto, M. S., Vahteristo, L. T., & Piironen, V. I. (2001). Applicability of microbiological assay and affinity chromatography purification followed by high-performance liquid chromatography (HPLC) in studying folate contents in rye. *J. Sci. Food Agric.*, *81*, 938–942.

Kariluoto, S., Liukkonen, K. H., Myllymäki, O., Vahteristo, L., Kaukovirta-Norja, A., & Piironen, V. (2006). Effect of germination and thermal treatments on folates in rye. *J. Agric. Food Chem.*, *54*, 9522–9528.

Katan, M. B., & De Roos, N. M. (2004). Promises and problems of functional foods. *Crit. Rev. Food Sci. Nutr.*, *44*, 369–377.

Kaur-Sawhney, R., Shih, L. M., & Galston, A. W. (1982). Relation of Polyamine Biosynthesis to the Initiation of Sprouting in Potato Tubers. *Plant Physiol.*, *69*, 411–415.

Keijbets, M. J. H., & Ebbenhorst-Seller, G. (1990). Loss of vitamin C (L-ascorbic acid) during long-term cold storage of Dutch table potatoes. *Potato Research*, *33*, 125–130.

Konings, E. J., Roomans, H. H., Dorant, E., Goldbohm, R. A., Saris, W. H., & van den Brandt, P. A. (2001). Folate intake of the Dutch population according to newly established liquid chromatography data for foods. *Am. J. Clin. Nutr.*, *73*, 765–776.

Krits, P., Fogelman, E., & Ginzberg, I. (2007). Potato steroidal glycoalkaloid levels and the expression of key isoprenoid metabolic genes. *Planta* .

Kupchan, S. M., Barboutis, S. J., Knox, J. R., & Cam, C. A. (1965). Beta-solamarine: tumor inhibitor isolated from Solanum dulcamara. *Science*, *150*, 1827–1828.

Laing, W. A., Wright, M. A., Cooney, J., & Bulley, S. M. (2007). The missing step of the L-galactose pathway of ascorbate biosynthesis in plants, an L-galactose guanyltransferase, increases leaf ascorbate content. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(22), 9534–9539.

Larsson, S. C., Virtanen, M. J., Mars, M., Mannisto, S., Pietinen, P., Albanes, D., & Virtamo, J. (2008). Magnesium, calcium, potassium, and sodium intakes and risk of stroke in male smokers. *Arch. Intern. Med.*, *168*, 459–465.

Lavie, Y., Harel-Orbital, T., Gaffield, W., & Liscovitch, M. (2001). Inhibitory effect of steroidal alkaloids on drug transport and multidrug resistance in human cancer cells. *Anticancer Res.*, *21*, 1189–1194.

Lee, K. R., Kozukue, N., Han, J. S., Park, J. H., Chang, E. Y., Baek, E. J., Chang, J. S., & Friedman, M. (2004). Glycoalkaloids and metabolites inhibit the growth of human colon (HT29) and liver (HepG2) cancer cells. *J. Agric. Food Chem.*, *52*, 2832–2839.

Legrand, D., & Scheen, A. J. (2007). Does coffee protect against type 2 diabetes? *Rev Med Liege*, *62*, 554–559.

Lewis, C. E., Walker, J. R. L., Lancaster, J. E., & Sutton, K. H. (1998). Determination of anthocyanins, flavonoids and phenolic acids in potatoes. I. Coloured cultivars of Solanum tuberosum L. *Journal of the Science of Food and Agriculture*, *77*, 45–57.

Liang, C. H., Shiu, L. Y., Chang, L. C., Sheu, H. M., Tsai, E. M., & Kuo, K. W. (2008). Solamargine enhances HER2 expression and increases the susceptibility of human lung cancer H661 and H69 cells to trastuzumab and epirubicin. *Chem. Res. Toxicol.*, *21*, 393–399.

Lisinka, G., & Leszczynski, W. (1989). *Potato Science and Technology*. Elsevier, London & New York, pp. 41–42.

Lopez, A. B., Van Eck, J., Conlin, B. J., Paolillo, D. J., O'Neill, J., & Li, L. (2008). Effect of the cauliflower Or transgene on carotenoid accumulation and chromoplast formation in transgenic potato tubers. *J. Exp. Bot.*, *59*, 213–223.

Love, S. L. S., T.; Shafii, B., Price, W. J., Mosley, A. R., & Thornton, R. E. (2004). Stability of expression and concentration of ascorbic acid in North American potato germplasm. HortScience 39, 156–160.

Lu, S., Van Eck, J., Zhou, X., Lopez, A. B., O'Halloran, D. M., Cosman, K. M., Conlin, B. J., Paolillo, D. J., Garvin, D. F., Vrebalov, J., Kochian, L. V., Kupper, H., Earle, E. D., Cao, J., & Li, L. (2006). The cauliflower Or gene encodes a DnaJ cysteine-rich domain-containing protein that mediates high levels of beta-carotene accumulation. *Plant Cell*, *18*, 3594–3605.

Malmberg, A., & Theander, O. (1985). Determination of Chlorogenic Acid in Potato Tubers. *Journal of Agricultural and Food Chemistry*, *33*, 549–551.

Manach, C., Scalbert, A., Morand, C., Remesy, C., & Jimenez, L. (2004). Polyphenols: food sources and bioavailability. *Am. J. Clin. Nutr.*, *79*, 727–747.

Matsuda, F., Morino, K., Ano, R., Kuzawa, M., Wakasa, K., & Miyagawa, H. (2005). Metabolic flux analysis of the phenylpropanoid pathway in elicitor-treated potato tuber tissue. *Plant Cell Physiol.*, *46*, 454–466.

McCue, K. F., Allen, P. V., Shepherd, L. V. T., Blake, A., Maccree, M. M., Rockhold, D. R., Novy, R. G., Stewart, D., Davies, H. V., & Belknap, W. R. (2007). Potato glycosterol rhamnosyltransferase, the terminal step in triose side-chain biosynthesis. *Phytochemistry*, *68*, 327–334.

McCue, K. F., Shepherd, L. V. T., Allen, P. V., Maccree, M. M., Rockhold, D. R., Corsini, D. L., Davies, H. V., & Belknap, W. R. (2005). Metabolic compensation of steroidal glycoalkaloid biosynthesis in transgenic potato tubers: using reverse genetics to confirm the in vivo enzyme function of a steroidal alkaloid galactosyltransferase. *Plant science*, *168*, 267–273.

McGuire, R. G. K., A. (1986). Calcium in potato tuber cell walls in relation to tissue maceration by Erwinia carotovora pv. atroseptica. Phytopathology 76, 401–406.

McKillop, D. J., Pentieva, K., Daly, D., McPartlin, J. M., Hughes, J., Strain, J. J., Scott, J. M., & McNulty, H. (2002). The effect of different cooking methods on folate retention in various foods that are amongst the major contributors to folate intake in the UK diet. *Br. J. Nutr.*, *88*, 681–688.

McMillan, M., & Thompson, J. C. (1979). An outbreak of suspected solanine poisoning in schoolboys: Examinations of criteria of solanine poisoning. *Q. J. Med.*, *48*, 227–243.

McNulty, H., & Pentieva, K. (2004). Folate bioavailability. *Proc. Nutr. Soc.*, *63*, 529–536.

Melse-Boonstra, A., Verhoef, P., Konings, E. J., Van Dusseldorp, M., Matser, A., Hollman, P. C., Meyboom, S., Kok, F. J., & West, C. E. (2002). Influence of processing on total, monoglutamate and polyglutamate folate contents of leeks, cauliflower, and green beans. *J. Agric. Food Chem.*, *50*, 3473–3478.

Mensinga, T. T., Sips, A. J., Rompelberg, C. J., van Twillert, K., Meulenbelt, J., van den Top, H. J., & van Egmond, H. P. (2005). Potato glycoalkaloids and adverse effects in humans: an ascending dose study. *Regul. Toxicol. Pharmacol.*, *41*, 66–72.

Moehs, C. P., Allen, P. V., Friedman, M., & Belknap, W. R. (1997). Cloning and expression of solanidine UDP-glucose glucosyltransferase from potato. *Plant Journal: for Cell and Molecular Biology*, *11*, 227–236.

Mondy, N. I., & Leja, M. (1986). Effect of mechanical injury on the ascorbic acid content of potatoes. *Journal of Food Science*, *51*, 355–357.

Monteiro, M., Farah, A., Perrone, D., Trugo, L. C., & Donangelo, C. (2007). Chlorogenic acid compounds from coffee are differentially absorbed and metabolized in humans. *J. Nutr.*, *137*, 2196–2201.

Morris, S. C., & Lee, T. H. (1984). The toxicity and teratogenicity of Solanaceae glycoalkaloids, particularly those of the potato (Solanum tuberosum): a review. *Food technology in Australia*, *36*, 118–124.

Morris, W. L., Ducreux, L., Griffiths, D. W., Stewart, D., Davies, H. V., & Taylor, M. A. (2004). Carotenogenesis during tuber development and storage in potato. *J. Exp. Bot.*, *55*, 975–982.

Nara, K., Miyoshi, T., Honma, T., & Koga, H. (2006). Antioxidative activity of bound-form phenolics in potato peel. *Biosci. Biotechnol. Biochem.*, *70*, 1489–1491.

Niggeweg, R., Michael, A. J., & Martin, C. (2004). Engineering plants with increased levels of the antioxidant chlorogenic acid. *Nat. Biotechnol.*, *22*, 746–754.

Nogueira, T., & do Lago, C. L. (2007). Determination of caffeine in coffee products by dynamic complexation with 3,4-dimethoxycinnamate and separation by CZE. *Electrophoresis*, *28*, 3570–3574.

Orphanos, P. I. (1980). Dry matter content and mineral composition of potatoes grown in Cyprus. *Potato Res.*, *23*, 371–374.

Orsomando, G., de la Garza, R. D., Green, B. J., Peng, M., Rea, P. A., Ryan, T. J., Gregory, J. F. 3rd, & Hanson, A. D. (2005). Plant gamma-glutamyl hydrolases and folate polyglutamates: characterization, compartmentation, and co-occurrence in vacuoles. *J. Biol. Chem.*, *280*, 28877–28884.

Parr, A. J., & Bolwell, G. P. (2000). Phenols in the plant and in man. The potential for possible nutritional enhancement of the diet by modifying the phenols content or profile. *Journal of the Science of Food and Agriculture*, *80*, 985–1012.

Parr, A. J., Mellon, F. A., Colquhoun, I. J., & Davies, H. V. (2005). Dihydrocaffeoyl polyamines (kukoamine and allies) in potato (Solanum tuberosum) tubers detected during metabolite profiling. *J. Agric. Food Chem.*, *53*, 5461–5466.

Plannels, E., Sanchez, C., Montellano, M. A., Mataix, J., & Llopis, J. (2003). Vitamins B6 and B12 and folate status in an adult Mediterranean population. *Eur. J. Clin. Nutr.*, *57*, 777–785.

Rajananthanan, P., Attard, G. S., Sheikh, N. A., & Morrow, W. J. (1999). Novel aggregate structure adjuvants modulate lymphocyte proliferation and Th1 and Th2 cytokine profiles in ovalbumin immunized mice. *Vaccine*, *18*, 140–152.

Randhawa, K. S., Sandhu, K. S., kaur, G., & Singh, D. (1984). Studies of the evaluation of different genotypes of potato (Solanum tuberosum L) for yield and mineral contents. *Plant Foods for Human Nutrition*, *34*(4), 239–242.

Rébeillé, F., Neuburger, M., & Douce, R. (1994). Interaction between glycine decarboxylase, serine hydroxymethyltransferase and tetrahydrofolate polyglutamates in pea leaf mitochondria. *Biochem. J.*, *302*, 223–228.

Rébeillé, F., Ravanel, S., Jabrin, S., Douce, R., Storozhenko, S., & Van Der Straeten, D. (2006). Folates in plants: biosynthesis, distribution, and enhancement. *Physiol. Plant.*, *126*, 330–342.

Reddivari, L., Vanamala, J., Chintharlapalli, S., Safe, S. H., & Miller, J. C. Jr. (2007). Anthocyanin fraction from potato extracts is cytotoxic to prostate cancer cells through activation of caspase-dependent and caspase-independent pathways. *Carcinogenesis*, *28*, 2227–2735.

Rivero, R. C., Hernandez, P. S., Rodríguez, E. M. R., Martín, J. D., & Romero, C. D. (2003). Mineral concentrations in cultivars of potatoes. *Food Chem.*, *83*, 247–253.

Roddick, J. G., Weissenberg, M., & Leonard, A. L. (2001). Membrane disruption and enzyme inhibition by naturally-occurring and modified chacotriose-containing Solanum steroidal glycoalkaloids. *Phytochemistry*, *56*, 603–610.

Rogan, G. J., Bookout, J. T., Duncan, D. R., Fuchs, R. L., Lavrik, P. B., Love, S. L., Mueth, M., Olson, T., Owens, E. D., Raymond, P. J., & Zalewski, J. (2000). Compositional analysis of tubers from insect and virus resistant potato plants. *Journal of Agricultural and Food Chemistry*, *48*, 5936–5945.

Scalbert, A., Manach, C., Morand, C., Remesy, C., & Jimenez, L. (2005). Dietary polyphenols and the prevention of diseases. *Crit. Rev. Food Sci. Nutr.*, *45*, 287–306.

Scurrah, M., Amoros, W., Burgos, G., Schafleitner, R., & Bonierbale, M. (2007). Back to the future: Millennium traits in native varieties. In: VI International Solanaceae Conference: Genomics Meet Biodiversity.

Scott, J. M. (1999). Folate and vitamin B12. *Proc. Nutr. Soc.*, *58*, 441–448.

Scott, J., Rebeille, F., & Letcher, J. (2000). Folic acid and folates: the feasibility for nutritional enhancement in plant foods. *J. Sci. Food Agric.*, *80*, 795–804.

Shih, Y. W., Chen, P. S., Wu, C. H., Jeng, Y. F., & Wang, C. J. (2007). Alpha-chaconine-reduced metastasis involves a PI3K/Akt signaling pathway with downregulation of NF-kappaB in human lung adenocarcinoma A549 cells. *J. Agric. Food Chem.*, *55*, 11035–11043.

Sinden, S. L., Deahl, K. L., & Aulenbach, B. B. (1976). Effect of glycoalkaloids and phenolics on potato flavor. *Journal of Food Science*, *41*, 520–523.

Sotelo, A., & Serrano, B. (2000). High-performance liquid chromatographic determination of the glycoalkaloids alpha-solanine and alpha-chaconine in 12 commercial varieties of Mexican potato. *J. Agric. Food Chem.*, *48*, 2472–2475.

Spinneker, A., Sola, R., Lemmen, V., Castillo, M. J., Pietrzik, K., & Gonzalez-Gross, M. (2007). Vitamin B6 status, deficiency and its consequences–an overview. *Nutr. Hosp.*, *22*, 7–24.

Spooner, D. M., McLean, K., Ramsay, G., Waugh, R., & Bryan, G. J. (2005). A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(41), 14694–14699.

Stapleton, A., Allen, P. V., Friedman, M., & Belknap, W. R. (1991). Purification and characterization of solanidine glycosyltransferase from the potato (Solanum tuberosum). *Journal of Agricultural and Food Chemistry*, *39*, 1187–1193.

Stenzel, O., Teuber, M., & Drager, B. (2006). Putrescine N-methyltransferase in Solanum tuberosum L., a calystegine-forming plant. *Planta*, *223*, 200–212.

Storozhenko, S., De Brouwer, V., Volckaert, M., Navarrete, O., Blancquaert, D., Zhang, G. F., Lambert, W., & Van Der Straeten, D. (2007). Folate fortification of rice by metabolic engineering. *Nat. Biotechnol.*, *25*, 1277–1279.

Strålsjö, L. M., Witthöft, C. M., Sjöholm, I. M., & Jägerstad, M. I. (2003). Folate content in strawberries (Fragaria x ananassa): effects of cultivar, ripeness, year of harvest, storage, and commercial processing. *J. Agric. Food Chem.*, *51*, 128–133.

Swain, J. F., McCarron, P. B., Hamilton, E. F., Sacks, F. M., & Appel, L. J. (2008). Characteristics of the diet patterns tested in the optimal macronutrient intake trial to prevent heart disease (OmniHeart): options for a healthy diet. *J. Am. Diet. Assoc.*, *108*, 257–265.

Tambasco-Studart, M., Titiz, O., Raschle, T., Forster, G., Amrhein, N., & Fitzpatrick, T. B. (2005). Vitamin B6 biosynthesis in higher plants. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(38), 13687–13692.

Tan, J. S., Wang, J. J., Flood, V., Rochtchina, E., Smith, W., & Mitchell, P. (2008). Dietary antioxidants and the long-term incidence of age-related macular degeneration: the Blue Mountains Eye Study. *Ophthalmology*, *115*, 334–341.

Tanemura, Y., & Yoshino, M. (2006). Regulatory role of polyamine in the acid phosphatase from potato tubers. *Plant Physiol. Biochem.*, *44*, 43–48.

Theodoratou, E., Farrington, S. M., Tenesa, A., McNeill, G., Cetnarskyj, R., Barnetson, R. A., Porteous, M. E., Dunlop, M. G., & Campbell, H. (2008). Dietary vitamin B6 intake and the risk of colorectal cancer. *Cancer Epidemiol. Biomarkers Prev.*, *17*, 171–182.

True, R. H., Hogan, J. M., Augustin, J., Johnson, S. J., Teitzel, C., Toma, R. B., & Shaw, R. L. (1978). Mineral composition of freshly harvested potatoes. *Am. Potato J.*, *55*(9), 511–519.

True, R. H., Hogan, J. M., Augustin, J., Johnson, S. J., Teitzel, C., Toma, R. B., & Orr, P. (1979). Mineral composition of freshly harvested potatoes. *Am. Potato J.*, *56*(7), 339–350.

Tosun, B. N., & Yücecan, S. (2008). Influence of commercial freezing and storage on vitamin C content of some vegetables. *International Journal of Food Science & Technology*, *43*(2), 316–321.

Tudela, J. A., Cantos, E., Espin, J. C., Tomas-Barberan, F. A., & Gil, M. I. (2002a). Induction of antioxidant flavonol biosynthesis in fresh-cut potatoes. Effect of domestic cooking. *J. Agric Food Chem.*, *50*, 5925–5931.

Tudela, J. A., Espin, J. C., & Gil, M. I. (2002b). Vitamin C retention in fresh-cut potatoes. *Postharvest Biology and Technology*, *26*, 75–84.

Tulipani, S., Mezzetti, B., Capocasa, F., Bompadre, S., Beekwilder, J., de Vos, C. H., Capanoglu, E., Bovy, A., & Battino, M. (2008). Antioxidants, phenolic compounds, and nutritional quality of different strawberry genotypes. *J. Agric. Food Chem.*, *56*, 696–704.

USDA National Nutrient Database for Standard Reference (SR20) http://www.ars.usda.gov/main/site_main.htm?modecode=12354500.

Vahteristo, L., Lehikoinen, K., Ollilainen, V., & Varo, P. (1997). Application of an HPLC assay for the determination of folate derivatives in some vegetables, fruits and berries consumed in Finland. *Food Chemistry*, *59*(4), 589–597.

Valkonen, J. P. T., Keskitalo, M., Vasara, T., & Pietila, L. (1996). Potato glycoalkaloids: a burden or a blessing? *Critical Reviews in Plant Sciences*, *15*(1), 1–20.

Werij, J. S., Kloosterman, B., Celis-Gamboa, C., de Vos, C. H., America, T., Visser, R. G., & Bachem, C. W. (2007). Unravelling enzymatic discoloration in potato through a combined approach of candidate genes, QTL, and expression analysis. *Theor. Appl. Genet.*, *115*, 245–252.

Wheeler, G. L., Jones, M. A., & Smirnoff, N. (1998). The biosynthetic pathway of vitamin C in higher plants. *Nature (London, England) Nature*, *393*, 365–369.

Wilson, G. S. (1959). A small outbreak of solanine poisoning. *Mon. Bull. Minist. Health Public Health Lab. Serv.*, *18*, 207–210.

Wills, R. B. H., Lim, J. S. K., & Greenfield, H. (1984). Variation in nutrient composition of Australian retail potatoes over a 12-month period. *J. Sci. Food Agric.*, *35*, 1012–1017.

Wolucka, B. A., & Montagu, M. v. (2007). The VTC2 cycle and the de novo biosynthesis pathways for vitamin C in plants: An opinion. *Phytochemistry*, *68*(21), 2602–2613.

Yamaguchi, T., Chikama, A., Mori, K., Watanabe, T., Shioya, Y., Katsuragi, Y., & Tokimitsu, I. (2007). Hydroxyhydroquinone-free coffee: A double-blind, randomized controlled dose-response study of blood pressure. *Nutr. Metab. Cardiovasc. Dis.*

Zimowski, J. (1991). Occurrence of a glucosyltransferase specific for solanidine in potato plants. *Phytochemistry*, *30*(6), 1827–1831.

Further reading

Avioli, L. V. (1988). Calcium and phosphorus. In: M. E. Shils, E. Young (Eds.), *Modern nutrition in health and disease*, (7th Edn) (pp. 142–158). Lea & Febiger, Philadelphia.

Bamberg, J. P., Peterson, L. A., Martin, M., & Krueger, A. R. (1998). Fine screening potato (Solanum) species germplasm for tuber calcium. *American Journal of Potato Research*, *75*, 181–186.

Cieslik, E., & Sikora, E. (1998). Correlation between the levels of nitrates and nitrites and the contents of potassium, calcium and magnesium in potato tubers. *Food Chem.*, *63*(4), 525–528.

Munne-Bosch, S., Weiler, E. W., Alegre, L., Muller, M., Duchting, P., & Falk, J. (2006). alpha-Tocopherol may influence cellular signaling by modulating jasmonic acid levels in plants. *Planta* .

Prat, S., Frommer, W. B., Hofgen, R., Keil, M., Kobmann, J., Koster-Topfer, M., Liu, X. J., Muller, B., Pena-Cortes, H., Rocha-Sosa, M., Sanchez-Serrano, J. J., Sonnewald, U., & Willmitzer, L. (1990). Gene expression during tuber development in potato plants. FEBS Lett. 268, 334–338.

Sánchez-Castillo, C. P., Dewey, P. J. S., Aguirre, A., Lara, J. J., Vaca, R., de la Barra, P. L., Ortiz, M., Escamilla, I., & James, W. P. T. (1998). The minerals of Mexican fruits and vegetables. *J. Food Composition and Analysis*, *11*, 340–356.

Tawfik, A. A., Kleinhenz, M. D., & Palta, J. P. (1996). Application of calcium and nitrogen for mitigating heat stress effects on potatoes. *American Potato Journal*, *73*, 261–273.

Vreugdenhil, D., Aarts, M. G. M., Koornneef, M., Nelissen, H., & Ernst, W. H. O. (2004). Natural variation and QTL analysis for cationic mineral content in seeds of Arabidopsis thaliana. *Plant, Cell & Environment*, *27*, 828–839.